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Short-Term Responses of Tree Growth Rings in Natural Gaps for Forest Management

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ABSTRACT

Objective: Effects of treefall gaps on tree radial growth pattern and vessel size plastisity were evaluated in cross sections of stems of moist tropical upland forest trees at Amazonas state, Brazil. Growth rings and vessel area of trees growing on 15 natural gaps in primary forest aged ≥ 4 years were studied macroscopically. **Method:** For determine growth periodicity, anatomy feature and study growth patterns of difference natural species, incisions made in the vascular cambium (Mariaux windows) was applicated. Analyses were performed on data of the community as a whole, and divided according to successional stage and vertical stratum to understand tree growth response. **Results:** Growth rings of 175 among 226 species sampled (77 %) were visible with and without the use of a 10 x lens. The vast majority (127 species, 73 %) formed rings by fiber dimensions (lumen area), whereas 18 species (10 %) formed rings by vessel size and frequency. After gap formation, mean ring width of 384 individuals of 115 species increased from 1.77 ± 0,04 to 2.46 ± 0.06 mm year^{-1} ($P < 0.001$), and mean vessel area of 399 individuals of 148 species increased from 0.062 ± 0.002 to 0.071 ± 0.004 mm^{2} mm^{-2} year^{-1} ($P < 0.001$). Variation in growth ring and vessel area was more evident in small individuals in larger gaps. **Conclusion:** The applicated method for visualize difference of change in anatomy feature of each specie and group of successional, of canopy position, was viable, comparing befor and after gap formations time.

Keywords: Growth Periodicity, Vessel Area, Treefall gap, Upland Primary Moist Forest, Amazonia.

INTRODUCTION

Tree rings and forest dynamics in treefall gaps were investigated in central Amazonia. In late successional and climax forests, juvenile tree individuals wait for the occurrence of natural disturbances to grow (WHITMORE, 1975). How advanced tree regeneration response to gap opening is our interesse and necessity to improve juvenile stand growth after logging that was not yet stablished as sustainable method in Amazon region. Many studies have documented tree growth response to gap formation in mature forests, either formed naturally or by logging (MONTGOMERY and CHAZDON, 2002; HERAULT *et al.*, 2010; D'OLIVEIRA and RIBAS, 2011; Ouriqui *et al.*, 2014; Machado *et al.*, 2015). However, for apply these studies to forest management more efficient, we have to observe the relation enter tree growth pattern and environmental changing factors, since growth rate varies with tree diameter, gap size, and interactions within the tree community. This research had aim to understand the growth pattern observing wood anatomy feature, growth rings at group and specie level. Even in the tropics with small seasonal variation, macroscopic growth ring features have been described for many species (Vetter and Botosso, 1989; Vetter, 2000; Worbes *et al.*, 2003; Schöngart, 2008; Miranda *et al.* 2017; Lópes & Villalba 2020; Worbes and Schöngart 2019). Nevertheless, research on the response of these features to environmental variation is still at an incipient stage (Moya and Tomazello, 2007; Brienen *et al.* 2010), and the response of tropical tree ring and vessel parameters have not been investigated in the tropics. Relating stem cross sectional wood anatomical features with individual level response to gap dynamics is very important for the interpretation of growth pattern studies. Ring width is directly responsible for radial growth, whereas vessel cross section area is indirectly brought about by vertical stem growth and elongation of branches (Tyree and Ewers, 1991) reflecting physiological acclimation to improve water absorption near gaps. (Tsuchiya *et al.* 2006). Both parameters were compared with gap features. The results of this study can be applied to prescribe silvicultural treatments in forest management plans in the tropics.

MATERIAL AND METHODS

Study area

This study was conducted in primary upland ("terra-firme") moist forest at Novo Aripuanã municipality, Amazonas state, Brazil (S 5°18', W 60°04'). The climate type is Af by Köppen classification. Mean annual temperature is 26 °C, relative humidity is 85 %, and mean annual rainfall is 3,439 mm, with a clear difference between rainy and dry season (Novo Aripuanã National Water Agency meteorological station).

Experimental design and field measurements

We installed research plots which had formed at least five years after gap formation. Fifteen natural gaps were randomly selected in primary forest, five small (< 100 m^2), five intermediate (100-400 m^2), and five large (≥ 400 m^2). Gap size was measured at ground level (Runkle, 1982) because gaps close after few years at canopy level. All trees with diameter at breast height (DBH) ≥ 5 cm within the gap, including a zone of 4 m away from the edge (i.e., those actually and presumably influenced by the formation of the gap) were identified to the genus level, and species, whenever possible.

Tree growth ring and vessel area measurement

Stem surfaces were incised up to the cambium several times throughout one growing year cycle in order to detect growth periodicity in the beginning of the rainy and dry seasons (Mariaux's windows, Mariaux, 1967). Hereafter, we call this cycle of "one year" as growth ring. For macroscope observation of ring width and vessel area, wood cores were sampled using an increment borer (Mattson, Sweden) and stem discs were collected (a whole disc or a half to observe the wound in the cambium). Cores and discs were photographed with a digital camera mounted on a macroscope Carton C-011. Ring widths were measured with Adobe Photoshop software. For each species, anatomical features were observed, and classified into one of four types of growth rings: 1) fiber, 2) parenchyma band, 3) ray, and 4) vessel (Vetter, 2000). This method was also used to determine gap age via cambium marking on advanced tree regeneration in the same gaps. Vessel area was calculated within four 1 mm^2 quadrats which were randomly selected for each year on images using Photoshop and AutoCAD (Release 15.2) software.

Data analysis

Growth ring width and vessel area were analyzed by Student's t-test ($P < 0.05$). The relationship between growth parameters and gap factors was analyzed by linear regression using Statistics Analysis System (SAS). Dependent variables used were: growth ring width variability ($GRW = (MRW_{time2} - MRW_{time1}) / MRW_{time1}$, MRW indicating mean growth ring width); vessel area variability ($VA = (MVA_{time2} - MVA_{time1}) / MVA_{time1}$, MVA indicating mean vessel area). GRW and VA were then classified according to: 1) DBH class (5-10 / 10-20 / 20-40 cm); and 2) tree height class (canopy / subcanopy species). Independent variables were: gap size (m^2), distance from gap center to tree canopy margin (m); distance from gap center to tree stem (m); Neighbor Index ($NI = (1\text{-}\log(Dis_{NB1}))^* DBH_{NB1} + (1\text{-}\log(Dis_{NB2}))^*DBH_{NB2}$, where

Dis_{NB1} and Dis_{NB2} stand for distance (m), and DBH_{NB1} and DBH_{NB2} stand for DBH (cm), 1 and 2 meaning the nearest and second nearest individuals).

RESULTS AND DISCUSSION

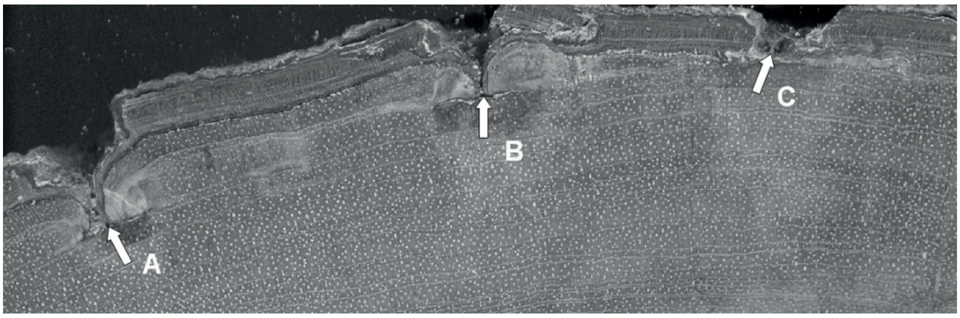
Forest and gap characteristics

Twelve among 15 gaps were created by trunk fall; the rest, by trunk break. They occupied 1.9 hectares of primary forest. The average size of small, medium, and large gaps were 75.5 m^2, 190.7 m^2, and 550.6 m^2, respectively. Based on growth ring counts, the age of the gaps varied from 4 to 11 years. A total of 2,007 tree individuals were inventoried and classified into 56 families, 186 genera, 692 morphospecies, and 16 unidentified species. Sapotaceae was the most numerous family (239 individuals), followed by Burseraceae, Mimosaceae, Lecythidaceae, Caesalpinaceae, and Annonaceae, decreasingly representative. These families accounted for 1,096 (43.5 %) individuals.

Macroscope observation

Effects of gap formation were investigated from Mariaux's windows and wood samples in the 175 among 226 species (77%) that had visible growth rings. Cambium marks were done on rather rainy and dry seasons to define periodicity (Fig. 1).

Fig. 1. The sequence of cambium marks in *Copaifera multijuga* (DBH = 30 cm). Incisions marked into cambium in the beginning of rainy season (**A**), dry season (**B**), and subsequent rainy season (**C**).



The main growth ring patterns in the tropics have been summarized by Vetter (2000).

Table 1. Growth ring patterns found in the species.

Growth periodicity type	N	%
fiber	78	44.6
parenchyma	42	24.0
fiber-parenchyma	34	19.4
fiber-vessel	13	7.4
parenchyma-vessel	3	1.7
fiber-ray	2	1.1
vessel	2	1.1
parenchyma-ray	1	0.6
fiber	175	100

Regarding growth ring boundaries, the fiber dimensions by lumen type (Fig. 2) was prevalent, present in 73 % of the species (Tab. 1). This majority growth periodicity type by fiber differentiation (Fig.2) coincide with reduction of number or lacking of vessels, as resultant of reduction of growth rithm: *Naucleopsis caloneura*, *Amaioua* sp.,*Unonopsis duckei, Paypaylora grandiflora, Siparuna cristata, Quiina negrensis*.

Fig. 2. Growth ring boundaries formed by fiber dimensions (lumen area) in: (**a**) *Naucleopsis caloneura* (10 x); (**b**) *Protium hebetatum* (30 x).

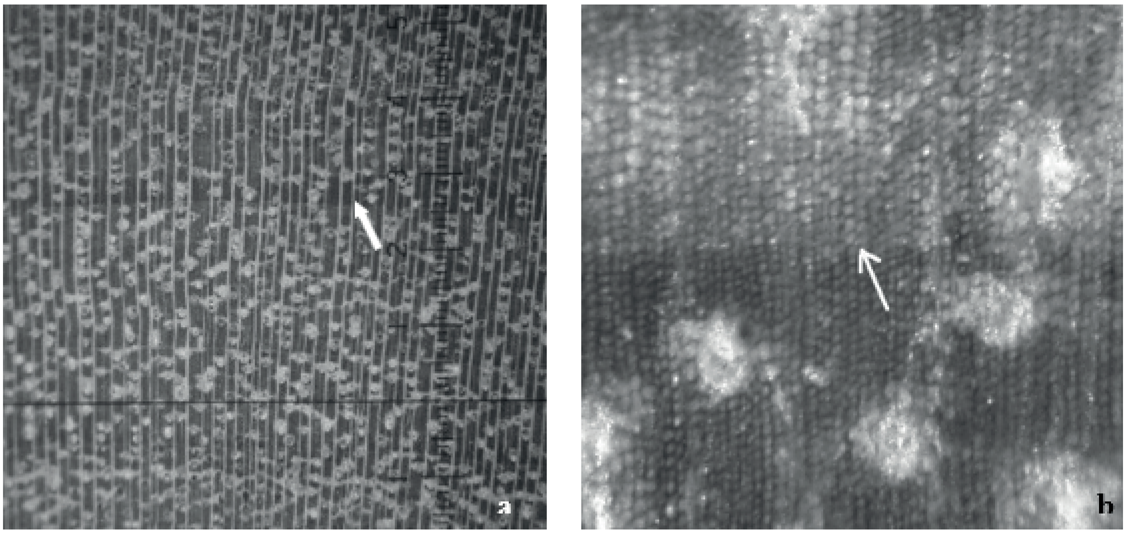


Table 2. shows wood anatomical features of the tree species studied, arranged by ecological group and forest vertical stratum occupied by the canopy. 43% of growth rings were clear among all species for which they were visible. Growth periodicity by vessel size and frequency change associated with fiber differentiation occurred in ten subcanopy intermediate/climax species. Only one canopy species, *Pouteria* sp. 2, showed growth periodicity by vessel change, but associated with parenchyma (Tab. 2).

Table 2. Anatomical and ecological characteristics of tree species

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
Anacardiaceae											
Anacardium	*parvifolium*	X	fiber		X		X		simple aliform	c	clx
Astronium	*le-cointei*		parenchyma		X			X	terminal parenchyma	c	clx
Annonaceae											
Anaxcogorea	*phaeocarpa*		fiber-ray		X			X	scalariform	sc	int
Bocageopsis	*multiflora*	X	parenchyma	X				X	scalariform	sc	int
Ephedranthus	*amazonicus*		fiber		X			X	scalariform	sc	clx
Fusaea	*longifolia*		fiber-vessel		X			X	scalariform	sc	int
Guatteria	*foliosa*	X	fiber		X			X	scalariform	sc	pio
	meliodora	X	fiber		X			X	scalariform	sc	
	sp. 1	X	fiber		X			X	scalariform	sc	
	sp. 2		fiber		X			X	scalariform	sc	
Malmea	*manausensis*		fiber		X			X	scalariform	sc	clx
Unonopsis	*duckei*		fiber		X			X	scalariform	sc	clx
	stipitata		vessel		X			X	scalariform	sc	
Burseraceae											
Protium	*apiculatum*		fiber			X	X		vasicentric scanty	c	clx
	divaricatum		fiber-parench.			X	X		vasicentric scanty	c	clx
	ferrugineum	X	fiber			X	X		vasicentric scanty	sc	clx
	gallosum		fiber			X	X		vasicentric scanty	sc	clx
	giganteum	X	fiber			X	X		vasicentric scanty	c	clx
	grandifolium		fiber-vessel			X	X		vasicentric scanty	sc	clx
	hebetatum		fiber			X	X		vasicentric scanty	sc	clx
	paniculatum		fiber			X	X		vasicentric scanty	sc	clx
	spruceanum		fiber			X	X		vasicentric scanty	c	clx
	strumosum	X	fiber			X	X		vasicentric scanty	sc	clx
	subserratum		fiber			X	X		vasicentric scanty	c	clx
	unifoliolatum		fiber-vessel			X	X		vasicentric scanty	sc	clx
	sp.		fiber			X	X		vasicentric scanty	sc	clx
Tetragastris	*panamensis*		fiber-vessel			X	X		vasicentric scanty	sc	clx
Caesalpiniaceae											
Cassia	*rubriflora*	X	fiber-parench.	X			X		aliform - confluent	sc	clx
Dialium	*guianense*		fiber-vessel			X	X		reticulate	sc	clx
Dimophandra	sp.	X	fiber-vessel		X		X		simple aliform		clx
Elizabetha	*speciosa*	X	fiber-parench.		X		X		simple aliform	sc	int
Eperua	*oleifera*		fiber			X	X		vasicentric scanty	c	clx
Hymenaea	sp.	X	fiber-parench.		X		X		aliform - unilateral		clx
Macrolobium	*limbatum*		fiber			X	X		simple aliform	c	clx
Peltogyne	*paniculata*	X	fiber-parench.		X		X		alif.- confluent - unilat.	c	int
Sclerolobium	*chrysophyllum*	X	fiber			X	X		vasicentric scanty	sc	int
	guianense	X	fiber			X	X		vasicentric scanty	sc	
	setiferum		fiber		X		X		simple aliform	c	int
	sp. 1	X	fiber		X		X		aliform - confluent	c	int
	sp. 2	X	fiber		X		X		aliform - confluent	c	int
Tachigali	sp.	X	fiber		X		X		aliform - confluent	sc	clx
Celasteraceae											
Maytenus	*guyanensis*	X	parenchyma		X			X	terminal parenchyma	sc	clx

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
Chrysobalanaceae											
Hirtella	*rodriguesii*		parenchyma		X		X		reticulate	sc	int
Licania	*apetala*		fiber		X		X		reticulate	c	clx
	octandra		parenchyma		X			X	reticulate	sc	int
	macrophylla		fiber-parench.		X		X		reticulate	sc	
	micrantha		fiber		X		X		reticulate	c	int
	sp.		fiber			X	X		vasicentric scanty		
Clusiaceae											
Tovomita		X	parench.-vessel		X		X		aliform - confluent	sc	int
Dichapetalaceae											
Tapura	*amazonica*		parench.-vessel		X		X		aliform - confluent	sc	clx
	guianensis		parenchyma		X		X		aliform - confluent	u	clx
	sp.		fiber		X		X		aliform - confluent		
Elaeocarpaceae											
Sloanea	*floribunda*		parenchyma		X			X	terminal parenchyma	sc	int
	sp. C	X	fiber-parench.			X		X	vasicentric scanty	c	
Euphorbiaceae											
Alchornea	*discolor*		fiber		X			X	reticulate	sc	int
Alchorneopsis	*floribunda*	X	fiber			X	X		vasicentric scanty	c	int
Dryptes	*variabilis*	X	fiber		X			X	scalariform	sc	clx
Mabea	*subsessilis*		fiber		X			X	terminal parenchyma	u	int
Senefeldera	*macrophylla*		parenchyma		X		X		terminal parenchyma	c	clx

Obs.) “parench.”: parenchyma, “lens”: visible by lens x10. “parat.”: paratracheal, “apot.”: apotracheal, “alif.”: aliform, “unilat.”: unilateral, “Strat.”: vertical stratum, “c”: canopy, “sc”: subcanopy, “u”: understory, “pio”: pioneer, “int”: intermediate, “clx”: climax.

Table 2.(cont.).

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
Fabaceae											
Andira	*unifoliolata*		fiber-parench.	X			X		aliforme confluente	c	clx
Diplotropis	*triloba*		parenchyma		X		X		simple aliform	c	int
Hymenolobium	*heterocarpum*		fiber-parench.		X		X		aliforme confluente	sc	int
	sp.		parenchyma		X		X		simple aliform	sc	int
Pterocarpus	*rohrii*		parenchyma		X		X		aliforme confluente	c	clx
Swartzia	*recurva*	X	parenchyma		X		X		aliforme confluente	c	clx
	tomentifera	X	fiber-parench.		X		X		aliforme confluente	c	clx
	sp.	X	fiber-parench.		X		X		simple aliform	c	clx
Flacourtiaceae											
Laetia	*procera*		fiber-vessel		X		X		terminal parenchyma	sc	pio
Humiriaceae											
Vantanea	*guianensis*		vessel		X		X		aliform - confluent	sc	int
	macrocarpa	X	fiber			X	X		vasicentric scanty	sc	int
Lauraceae											
Ocotea	*aciphylla*		fiber			X	X		vasicentric scanty	sc	int
	amazonica	X	fiber		X		X		simple aliform	u	int
	nigrescens	X	fiber			X	X		simple aliform	c	int
Lecythidaceae											
Couratari	*stellata*	X	fiber		X		X		reticulate	c	clx
Eschweilera	*carinata*	X	parenchyma	X			X		reticulate	c	clx

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
	collina		parenchyma	X				X	reticulate	c	clx
	grandiflora		parenchyma	X				X	reticulate	sc	clx
	pedicellata		parenchyma	X				X	reticulate	sc	clx
	tessmannii	X	parenchyma	X				X	reticulate	c	clx
	truncata	X	parenchyma	X				X	reticulate	c	clx
	wachenheimii		parenchyma	X				X	reticulate	sc	clx
	sp. 1		parenchyma	X				X	reticulate	sc	clx
	sp. 2		parenchyma		X			X	reticulate	sc	clx
	sp. 3		parenchyma		X			X	reticulate	sc	clx
Malvaceae											
Bombacaopsis	sp. 1	X	fiber-parench.		X		X		aliform - confluent	sc	int
	sp. 2		fiber		X		X		simple aliform	sc	
Quaralibea	*ochrocalyx*		fiber-ray		X			X	scalariform	sc	int
Scleronema	*micranthum*		parench.-ray	X				X	terminal parenchyma	sc	int
Sterculia	*duckeana*	X	fiber-parench.		X			X	terminal parenchyma	sc	int
	sp. 1	X	fiber-parench.		X			X	scalariform	sc	int
	sp. 2	X	fiber-parench.		X			X	reticulate	c	clx
Teobroma	*subincanum*	X	fiber		X			X	diffuse	sc	int
	sylvestre	X	fiber-parench.		X			X	terminal parenchyma	sc	int
Lueheopsis	*rosea*		fiber-parench.		X		X		reticulate	c	int
Meliaceae											
Carapa	*guianensis*	X	parenchyma		X		X	X	vasicentric - terminal	sc	int
Guarea	*cinnammomea*	X	fiber		X		X		aliform - confluent	c	
	sp.	X	fiber-vessel		X		X		aliform - confluent		
Trichilia	*schomburgkii*		parenchyma		X		X		aliform - terminal	sc	int
	pallida		parenchyma		X		X		aliform - terminal	sc	
Memecylaceae											
Mouriri	*angulicosta*	X	fiber			X	X		vasicentric scanty	sc	clx
	dimorphandra		fiber		X		X		diffuse	sc	
Mimosaceae											
Abarema	*jupunba*		fiber		X		X		simple aliform	sc	int
Inga	*bicoloriflora*		fiber-parench.	X			X		aliform - confluent	sc	int
	cordatoalata	X	fiber		X		X		simple aliform	sc	int
	huberi	X	fiber-parench.	X			X		aliform - confluent	c	int
	lateriflora	X	fiber		X		X		simple aliform	sc	int
	leiocalycina	X	fiber		X		X		simple aliform	sc	int
	obidensis		fiber	X			X		simple aliform	sc	int
	paraensis	X	fiber-parench.	X			X		aliform - confluent	c	int
	rubiginosa	X	fiber		X		X		simple aliform	sc	int
	thibaudiana	X	fiber		X		X		simple aliform	sc	int
Parkia	*discolor*	X	fiber		X		X		simple aliform	c	int
	multijuga	X	fiber		X		X		simple aliform	c	int
Zygia	*racemosa*	X	parenchyma	X			X		aliform - confluent	c	int
	sp.		fiber-parench.		X		X		simple aliform	c	int
Miristicaceae											
Iryanthera	*coriacea*		parenchyma		X			X	terminal parenchyma	sc	int
	juruensis		fiber-parench.		X			X	terminal parenchyma	sc	int
	sp.		fiber-parench.		X			X	terminal parenchyma	sc	int

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
Virola	*calophylla*	X	fiber			X	X		vasicentric scanty	sc	int
	venosa	X	fiber			X	X		vasicentric scanty	sc	int

Obs.) “parench.”: parenchyma, “lens”: visible by lens x10. “parat.”: paratracheal, “apot.”: apotracheal, “Strat.”: vertical stratum, “c”: canopy, “sc”: subcanopy, “u”: understory, “pio”: pioneer, “int”: intermediate, “clx”: climax.

Table 2.(cont.).

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
Moraceae											
Brosimum	sp.		fiber-parench.		X		X		simple aliform	c	clx
Clarisia	*racemosa*	X	parenchyma		X			X	aliform - confluent	c	clx
Helicostylis	*turbinata*	X	fiber		X			X	simple aliform		clx
Naucleopsis	*caloneura*		fiber		X		X		aliform - confluent	sc	int
	macrophylla		fiber			X	X		simple aliform		
	ulei		fiber		X		X		aliform - confluent	c	clx
Pseudolmedia	*laevis*		fiber-parench.		X		X		aliform - unilateral	c	clx
Myrtaceae											
Eugenia	*florida*	X	fiber-parench.		X		X		aliform - confluent	c	clx
	sp. 1	X	fiber-parench.		X		X		simple aliform	sc	clx
	sp. 2		fiber		X		X		aliform - confluent	sc	clx
	sp. 3		fiber		X		X		aliform - confluent	sc	clx
Ochnaceae											
Ouratea	*discophora*	X	fiber		X		X		aliform - confluent	sc	int
Olacaceae											
Aptandra	*tubicina*	X	fiber		X			X	scalariform	sc	int
Minquartia	*guianensis*		fiber		X		X		simple aliform	sc	clx
Quiinaceae											
Lacunaria	*jenmani*		fiber-vessel			X	X		vasicentric scanty	sc	clx
Quiina	*negrensis*		fiber			X	X		vasicentric scanty	sc	clx
Rubiaceae											
Amaioua	*guanensis*		fiber		X		X		aliform - confluent	u	clx
	sp.		fiber-vessel		X		X		aliform - confluent	sc	clx
Ferdinandusa	sp.		fiber-vessel			X	X		vasicentric scanty	sc	int
Rutaceae											
Zanthoxyllum	sp.	X	parenchyma	X				X	terminal parenchyma	sc	int
Sapindaceae											
Talisia	*allenii*		fiber-parench.		X		X		simple aliform	u	clx
Sapotaceae											
Chrysophyllum	*amazonicum*	X	parenchyma		X			X	reticulate	c	clx
Pouteria	*gardneri*	X	parenchyma		X			X	reticulate	c	clx
	campanulata	X	parenchyma		X			X	reticulate	c	clx
	filipes	X	parenchyma		X			X	reticulate	c	clx
	guianensis	X	parenchyma		X			X	reticulate	c	clx
	hispida	X	parenchyma		X			X	reticulate	c	clx
	oblanceolata		parenchyma		X			X	reticulate	sc	clx
	pallens		parenchyma		X		X		reticulate	c	clx
	platyphylla		parenchyma		X			X	reticulate	sc	clx
	reticulata		parenchyma		X			X	reticulate	c	clx
	torta		parenchyma		X			X	reticulate	c	clx

Species		Growth ring		Parenchyma						Strat.	Eco.
		Clear	Type	eye	lens	invisi	parat.	apot.	classification		Group
	sp. 1		fiber		X			X	reticulate	c	clx
	sp. 2		parench.-vessel		X		X		simple aliform	c	clx
	sp. 3		parenchyma		X			X	reticulate	c	clx
Sarcaulos	*brasiliensis*		parenchyma		X		X		reticulate	c	clx
Simaroubaceae											
Simaba	*cedron*	X	fiber-parench.	X				X	terminal parenchyma	sc	int
Simarouba	*amara*		fiber-parench.		X		X		simple aliform	sc	int
Siparunaceae											
Siparuna	*cristata*		fiber		X			X	scalariform	u	pio
	decipiens		fiber		X			X	scalariform	sc	clx
	guianensis		fiber		X			X	scalariform	u	
	monogyna		fiber		X			X	scalariform	sc	clx
	sp.		fiber		X			X	scalariform		
Urticaceae											
Cecropia	*sciadophylla*		fiber-parench.			X	X		vasicentric scanty	csc	pio
Pourouma	*bicolor*		fiber		X		X		diffuse	sc	pio
	ferruginea		fiber		X		X		simple aliform	sc	pio
	guianensis	X	fiber-parench.		X		X		aliform - vasicentric	sc	pio
	minor	X	fiber-parench.		X		X		aliform - vasicentric	c	pio
	velutina	X	fiber			X	X		vasicentric scanty	sc	pio
	villosa	X	fiber		X		X		aliform - vasicentric	sc	pio
Verbenaceae											
Vitex	*triflora*	X	fiber-vessel			X	X		vasicentric scanty	sc	int
Violaceae											
Leonia	*cymosa*		fiber-parench.		X		X		aliform - unilateral	sc	clx
Paypalora	*grandiflora*		fiber			X	X		simple aliform	sc	clx
	macrophylla		fiber			X	X		simple aliform	sc	clx
Rinorea	*racemosa*	X	fiber-vessel		X		X		simple aliform	u	clx

Obs.) “parench.”: parenchyma, “lens”: visible by lens x10. “parat.”: paratracheal, “apot.”: apotracheal, “Strat.”: vertical stratum, “c”: canopy, “sc”: subcanopy, “u”: understory, “pio”: pioneer, “int”: intermediate, “clx”: climax.

Growth ring width and gap formation

Growth ring width data for complete ten year series (five years before and after gap formation) were obtained for 384 individuals over 115 of 175 species. The five-year average growth ring width (one cycle of dry / rainy season) jumped from 1.77 mm y^{-1} (± 0.04 mm y^{-1}, $P < 0.05$) to 2.46 mm y^{-1} (± 0.06 mm y^{-1}, $P < 0.001$; Fig. 3a) after gap formation. The increase was evident in every stem diameter class (5-10 / 10-20 / 20-40 / > 40 cm) ($P < 0.001$; Fig. 3-b). Thus, ring growth decreased moderately in the subsequent year, and stabilized at a similar rate (Fig. 3b).

Fig. 3a. Mean growth ring width before and after gap formation, averaged by all 384 individuals over 115 species. In x axis, b_i, a_i: year i before and after gap formation, respectively; dashed line: time of gap formation.

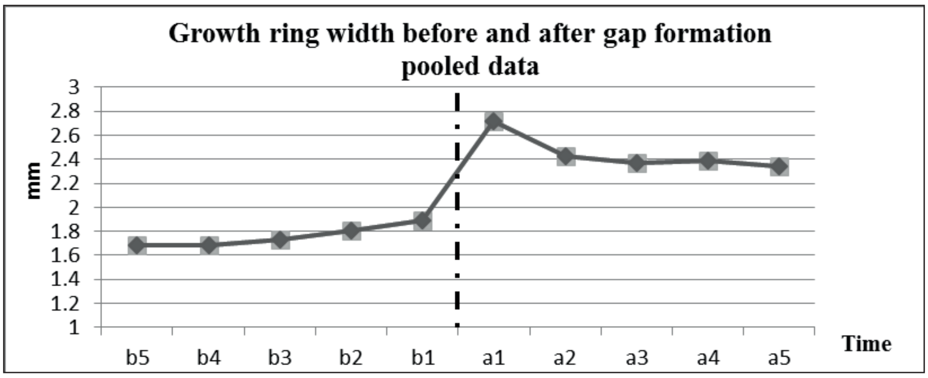
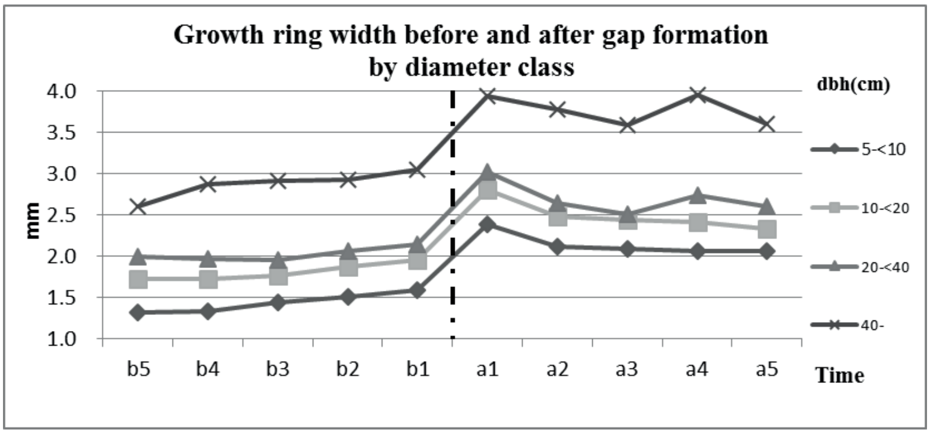


Fig. 3b. Mean growth ring width of individuals, classified by DBH. In x axis, b_i, a_i: year i before and after gap formation, respectively; dashed line: time of gap formation.



Mean ring growth before and after gap formation decreased as DBH increased (5-10 cm: 1.46 ± 0.04 to 2.14 ± 0.06 mm y^{-1}, $P < 0.001$; 10-20 cm: 1.81± 0.06 to 2.49 ± 0.08 mm y^{-1}, $P < 0.001$; 20-40 cm: 2.03 ± 0.12 to 2.70 ± 0.16 mm y^{-1}, $P < 0.001$; > 40 cm: 2.88 ± 0.25 to 3.77 ± 0.35 mm y^{-1}, $P < 0.001$). Also, variability of increase was higher in large DBH classes (Tab. 3).

Table 3. Tree growth ring width before and after gap formation in each DBH class.

DBH (cm)	5-10		10-20		20-40		> 40	
	before	after	before	after	before	after	before	after
Mean (mm y^{-1})	1.46	2.14	1.81	2.49	2.03	2.70	2.88	3.77
CI ($\alpha = 0.05$)	± 0.04	± 0.06	± 0.06	± 0.08	± 0.12	± 0.16	± 0.25	± 0.35

CI: confidence interval

Growth ring width significantly increased after gap formation for all DBH classes regardless of gap size, except for individuals with DBH > 40 cm in medium-sized gaps. This was more evident for small trees (Tab. 4).

Table 4. Mean tree ring width before and after gap formation in each DBH class and gap size.

Gap size		DBH			
		5 - < 10 cm	**10 - < 20 cm**	**20 - < 40 cm**	**≥ 40 cm**
Large	Before	1.44 (± 0.05)	1.77 (± 0.09)	2.11 (± 0.15)	2.57 (± 0.25)
	After	2.16 (± 0.08)	2.40 (± 0.12)	2.77 (± 0.19)	3.44 (± 0.34)
	Increase (%)	49.4	35.9	31.6	33.8
	P	< 0.001	< 0.001	< 0.001	< 0.001
Medium	Before	1.43 (± 0.10)	1.79 (± 0.11)	1.99 (± 0.29)	3.25 (± 0.49)
	After	2.14 (± 0.12)	2.52 (± 0.16)	2.69 (± 0.37)	3.63 (± 0.51)
	Increase (%)	49.5	41.1	35.3	11.7
	P	< 0.001	< 0.001	0.0018	0.1368
Small	Before	1.41 (± 0.10)	1.83 (± 0.17)	-	-
	After	2.09 (± 0.16)	2.52 (± 0.26)	-	-
	Increase (%)	44.9	37.2	-	-
	P	< 0.001	< 0.001	-	-

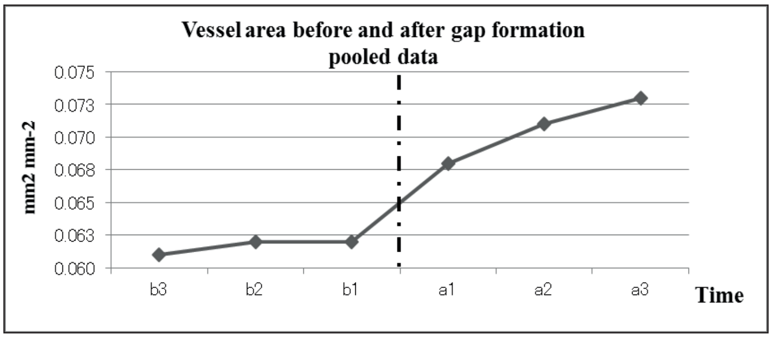
Values between brackets are confidence intervals ($\alpha = 0.05$). *P* value was calculated with Tukey test. For classes 20-40 cm and ≥ 40 cm in small gaps, the number of individuals was insufficient for analysis. "Increase (%)" means increase rate.

During five years after gap formation, mean ring growth in/near gaps (2.46 mm year^{-1}) was higher than in other studies in tropical forests at stable succession stages, which were at the 1-2 mm.year^{-1} range (Higuchi *et al.*, 1998; Worbes, 1999; Silva *et al.*, 2002; Chambers *et al.*, 2001; Clark *et al.*, 2003; Laurance *et al.*, 2004; Toledo *et al.*, 2011; Ouriqui *et al.*, 2014). This tells us that trees are stimulated by gap formation, and continue to grow a few years.

Vessel area and gap formation

Throughout the entire data set, mean vessel area increased from 0.062 mm^2 mm^{-2} year^{-1} (± 0,002; $\alpha = 0.05$) to 0.071 mm^2 mm^{-2} year^{-1} (± 0.004; $\alpha = 0.05$) after gap formation (Fig. 4).

Fig. 4. Mean vessel area before and after gap formation, averaged by all 399 individuals over 148 species. In x axis, b_i, a_i: year i before and after gap formation, respectively; dashed line: time of gap formation.



Therefore, vessel area change becomes clearer when the data are stratified by DBH class per gap size: small / medium / large. It significantly increased for individuals with 5 ≤ DBH < 10 cm and 10 ≤ DBH < 20 cm in large gaps. In medium-sized gaps, an increase was observed only for the class of 10 ≤ DBH < 20 cm. No significant variation was found for trees in any DBH class in small gaps (Tab. 5).

Table 5. Mean vessel area before and after gap formation in each DBH class and gap size.

Gap size		**DBH**			
		5 - < 10 cm	**10 - < 20 cm**	**20 - < 40 cm**	**≥ 40 cm**
Large	Before	0.054 (± 0.004)	0.061 (± 0.004)	0.072 (± 0.006)	0.101 (± 0.012)
	After	0.059 (± 0.004)	0.067 (± 0.004)	0.079 (± 0.007)	0.149 (± 0.056)
	Increase (%)	10.4	10.9	10.8	47.6
	P	0.0264	0.0137	0.0519	0.0534
Medium	Before	0.046 (± 0.005)	0.053 (± 0.004)	0.079 (± 0.014)	0.098 (± 0.025)
	After	0.050 (± 0.006)	0.061 (± 0.006)	0.085 (± 0.014)	0.119 (± 0.024)
	Increase (%)	9.3	14.4	7.2	22.8
	P	0.1469	0.0166	0.2774	0.0969
Small	Before	0.047 (± 0.007)	0.072 (± 0.01)	0.044 (± 0.012)	0.101 (± 0.015)
	After	0.048 (± 0.006)	0.074 (± 0.008)	0.049 (± 0.015)	0.098 (± 0.019)
	Increase (%)	0.2	2.6	10.2	-2.4
	P	0.4898	0.3902	0.3130	0.4166

Values between brackets are confidence intervals ($\alpha = 0.05$, in brackets). *P* value was calculated with Tukey test. “Increase (%)” means increase rate.

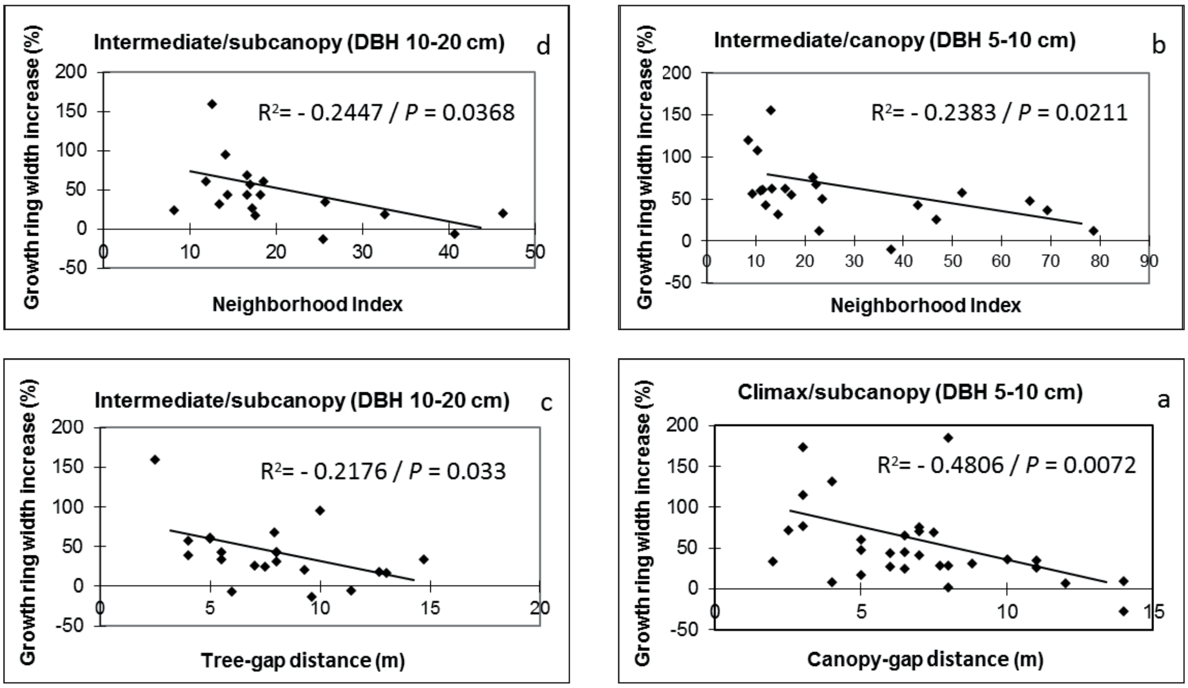
This result shows that elongation of stems and branches in smaller individuals is greater in large canopy openings, and results in increased vessel area. Trees of DBH ≥ 20 cm do not obviously respond to gap formation, although radial growth was significant for all DBH classes. It corresponde to the result of periodicity type that minority of species forms growth ring by vessel differentiation (Tab. 1).

Species response by successional group and position in canopy

For a more detailed understanding of the changes in growth ring width and vessel area at an occurrence of treefall gap, species were classified into four groups from the viewpoint of succession stage and position in canopy: 1) climax / canopy, 2) climax / subcanopy, 3) intermediate / canopy, 4) intermediate / subcanopy. Understory species were assigned to subcanopy categories. Regression test between tree ring growth by successional group / canopy position and environmental factors was analyzed for 115 species (n = 384).

With regard to growth ring width, small diameter classes (DBH = 5-20 cm) respond more to distance from gap and neighborhood index (Fig. 5a-d). This confirms the adequacy of thinning around juvenile stands or advanced regeneration of interest species to improve diametrical growth.

Fig. 5. Regression test between tree ring growth and environmental factors. Ring width is expressed as increase rate (%, n = 384 individuals, 115 species) after gap formation. “Canopy-Gap” = distance from gap center to margin of tree canopy; “Tree-Gap” = distance from gap center to tree stem base position.



Relationship between vessel area in stem cross sections and successional group / canopy position was analyzed for 143 species (n = 354). For vessel area increase, only intermediate / subcanopy species (10 ≤ DBH < 20 cm) and climax / subcanopy species (5 ≤ DBH < 10 cm) reached a significant level in the relationship with gap size ($R^2 = 0,1216$ / $P = 0.0236$; $R^2 = 0.1737$ / $P = 0.0274$, respectively).

Growth ring width and vessel area responded more distinctly to gap factors in intermediate successional species. Although pioneer and opportunistic species have a high plasticity to environmental change (Chazdon and Pearcy, 1986; Swaine and Whitmore, 1988), the results of this study shed detail into how stem size, position in canopy, and successional group are related to gap features. In the intermediate / subcanopy group, DBH = 10-20 cm, ring width, and vessel area were negatively correlated with distance to gap and neighborhood index. Ring width and vessel area are negatively correlated to distance to gap in the case of climax / subcanopy species, which can acclimate to microenvironmental changes. These species, e.g., *Eschweilera wachenheimii, Protium hebetatum*, *Rinorea racemosa, Amaioua guianensis,* were abundant in this study (67 % of individuals were in the climax/subcanopy group).

It is known that subcanopy tree species have a greater ability to absorb soil water in and near gaps (Kapos *et al.*, 1990; van Dam, 2001). In the present study, subcanopy species in both intermediate and climax successional groups tended to optimize vessel area in large gaps. Nevertheless, maintaining the hydric potential necessary to avoid embolism brings difficulties for larger individuals because gravity increases with height (Zimmermann, 1983; Thomas, 2000). Consequently, only juvenile trees (DBH = 5-10 cm) responded to gaps. Intermediate and climax canopy species demand open canopies. However, canopy species did not respond to gap factors, in particular, vessel area. This might be due to species-specific strategies mitigating vulnerability to embolism. For canopy species, growth ring boundary appears as a parenchyma band in cross section. The vessel distribution is the diffused porous, and vessel size does not change throughout the year. In subcanopy species, fiber density varies, but nothing changes in parenchyma. Therefore, growth rings were clearly different between the two groups (Tab. 2).

Species classification according to response to gap formation

Most tree species have naturally low frequency in Amazonian moist forests (Gentry, 1988). With some exceptions, abundant species can be classified into four groups based on the response of growth ring width and vessel area to gap formation (Tab. 6).

Table 6. Species classification according to response of growth ring width and vessel area to gap formation

Family	Genus	Specie	Stratum	Eco.Grp	DBH(cm)	Elong.
Species group 1: increase in ring width + increase in vessel area						
Lecythidaceae	*Eschweilera*	*tessimanii*	canopy	climax	≥20	X
Fabaceae	*Pterocarpus*	*rohrii*	canopy	climax	5-20	X
Moraceae	*Naucleopsis*	*ulei*	canopy	climax	5-20	X
Sapotaceae	*Pouteria*	*guianensis*	canopy	climax	5-20	X
Mimosaceae	*Inga*	*paraensis*	canopy	intermediate	5-20	
Myrtaceae	*Calycolpus*	spp	subcanopy	climax	5-20	
Chrysobalanaceae	*Licania*	spp	subcanopy	intermediate	5-20	
Species group 2: increase in ring width > increase in vessel area						
Anacardiaceae	*Astronium*	*lecointei*	canopy	climax	5-20	
Caesalpiniaceae	*Copaifera*	*multijuga*	canopy	climax	5-20	X
Fabaceae	*Swartzia*	*recurva*	canopy	climax	5-20	X
Lecythidaceae	*Eschweilera*	*tessimanii*	canopy	climax	5-20	X
Mimosaceae	*Zygia*	*racemosa*	canopy	climax	5-20	X
Sapotaceae	*Pouteria*	*campanulata*	canopy	climax	5-20	X
Sapotaceae	*Sarcaulos*	*brasiliensis*	canopy	climax	5-20	X
Mimosaceae	*Parkia*	*multijuga*	canopy	intermediate	5-20 / ≥20	X
Annonaceae	*Unonopsis*	spp	subcanopy	climax	5-20	
Burseraceae	*Protium*	spp	subcanopy	climax	5-20	
Dichapetalaceae	*Tapura*	spp	subcanopy	climax	5-20	
Myrtaceae	*Eugenia*	spp	subcanopy	climax	5-20	
Rubiaceae	*Amaioua*	spp	subcanopy	climax	5-20	
Violaceae	*Paypayrola*	spp	subcanopy	climax	5-20	
Siparunaceae	*Siparuna*	spp	subcanopy	?	5-20	
Bombacaceae	*Quaralibea*	*occhrocalyx*	subcanopy	intermediate	5-20	X
Mimosaceae	*Inga*	spp	subcanopy	intermediate	5-20	
Miristicaceae	*Iryanthera*	*coriacea*	subcanopy	intermediate	5-20	X
Sterculiaceae	*Sterculia*	spp	subcanopy	intermediate	5-20	
Species group 3: increase in vessel area > increase in ring width						
Violaceae	*Rinoria*	spp	subcanopy	climax	5-20	
Mimosaceae	*Inga*	*bicoloriflora*	subcanopy	intermediate	5-20	
Miristicaceae	*Iryanthera*	spp	subcanopy	intermediate	5-20	X

Family	Genus	Specie	Stratum	Eco.Grp	DBH(cm)	Elong.
Miristicaceae	*Virola*	*theiodora*	subcanopy	intermediate	5-20	X
Species group 4: no increase in ring width / vessel area						
Urticaceae	*Pourouma*	*villosa*	subcanopy	pioneira	5-20	X
Urticaceae	*Pourouma*	spp	subcanopy	pioneira	5-20	

“Stratum”: vertical stratum, “Eco.Grp”: ecological (successional) group, “Elong.”: species whose branches elongate into gap space.

The seven species composing Group 1 respond by both growth ring width and vessel area increase. These species have diffuse-porous vessel distribution. However, in this study, discontinuity of vessels was observed at an occurrence of canopy openness. These species elongate branches in search for light into canopy gaps, and consequently leaf area increases. This may bring about anatomical plasticity, such as increase of vessel area, to raise water intake, more than physiological plasticity, like stomatal control (Tyree and Ewers, 1991).

Inga paraensis is a colonizer species. A radial growth of 3.23 mm year^{-1} has been reported (Laurance *et al.*, 2004), and maximum age was estimated at 78 years (Holm *et al.*, 2014). In this study, DBH of juvenile individuals ranged from 5 to 10 cm, and increase rate was relatively small, although significant (from 1.25 to 2.65 mm year^{-1}, $P < 0.0001$). Likewise, growth ring width of *Licania* spp., a subcanopy species, increased from 1.42 to 1.81 mm year^{-1} (DBH: 5-20 cm), more than in *L. octandra* reported by Laurance *et al.* (2004: 0.73 mm year^{-1}).

The response of *Eschweilera tessimanii* varied with stem diameter. While individuals with DBH = 5-20 cm varied in radial growth, those with DBH ≥ 20 cm varied in radial growth and vessel area, suggesting that this canopy species shifted response strategy to gap microenvironment according to tree size.

Species such as *Astronium lecointei*, *Copaifera multijuga*, *Pouteria campanulata*, *Sarcaulos brasiliensis*, *Swartzia recurva*, *Zygia racemosa*, and *Parkia multijuga* reacted more conspicuously in growth ring width than in vessel area at gap openings. Most of them are climax species, and their crowns reach the height of forest canopy and subcanopy (Tab. 6). The strategy to maximize water transport efficiency lies in a homogeneous distribution of vessels. Small-sized vessels minimize risk of xylem embolism in extreme dry season conditions (Zimmermann, 1983). These species develop physiological plasticity, such as stomatal control, to optimize water translocation (Sarmiento *et al.*, 1985).

In contrast, in the case of individuals with DBH < 20 cm, subcanopy/climax species prioritize radial growth and reach their maximum inherent height (Tab. 6). Furthermore, fiber lumen in stem cross sections reflect radial growth of subcanopy individuals in gaps, while vessels are diffusely distributed with no change in size (Tab. 2).

Group 3 is composed predominantly of intermediate / subcanopy species which do not respond to gap formation by ring width (Tab. 6). Their life is spent under the canopy, with little solar radiation. Elongation of subcanopy branches was also frequently observed in *Iryanthera* spp and in *Virola* spp. However, branches of both species were verticillar. The pattern may not be driven by search for radiation in gap space. As to *Rinorea* spp., growing under the subcanopy, averaging 8.6 m in height and 8.9 cm in stem diameter (n = 55), on the other hand, we estimate that individuals with stem diameter smaller than 20 cm had already reached maturity.

For Group 1 and 3, the vessel area change was observed in gap opening. This means that these genera and species respond to increasing vessel area by changing soil water. Especially genus *Inga* changed in group 1 and 3, genus *Iryanthera* in group 2 and 3, *Eschweilera tessimani* in group 1 and 2 by different diameter size. They optimize the use of water as anatomical plasticity in gap opening, while many species do not change the vessel area. This aspect may explain that these species are more resistant to environmental changes. Among these species, *Inga* spp., all species studied with paratracheal parenchyma with simple aliforms - confluent (Tab. 6) can response more dynamically to environmental changes such as opening of gaps.

Group 4 is composed of pioneer species only, which expand vessel area at an occurrence of treefall gap (Tab. 6). Most individuals have thin stems, but primary growth is quite high, suggesting that it is primarily associated with optimization through architectural change. Phillips *et al.* (2001) reported that gap colonizing species *Simarouba amara* and *Tapirira guianensis* optimize hydraulic conductivity through change in leaf area via physiological plasticity in stomatal opening. Leaf area is highly correlated with hydraulic conductivity in xylem in order to assure water translocation (Tyree and Ewers, 1991). Thus, they respond to gap opening faster than all other species.

■ CONCLUSION

Average tree growth in treefall gaps (2.46 mm year^{-1}) was high compared with other results for the tropics. The most representative species in the gaps studied were sensitive to gap formation: growth ring width and mean vessel area increased right after gap opening, although variation was lower in the latter. Species showed different response strategies to gap size and distance from gap to stand (gap factors) according to successional position (ecological group) and canopy position: while species in the subcanopy intermediate/climax group responded to gap opening through growth ring width and vessel area increase, for those in the canopy intermediate group, growth ring width increased by reducing competition among individuals in gaps rather than as a response to gap factors. At the species level, some immediately changed growth ring width and/or vessel area in response to gap formation, whereas others did not respond at all. Basically, however, since gaps generate competition among individual trees, gap study is indispensable to tropical forest management and silviculture.

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